Some Observations on the Hypophysis of Petromyzon and of Amia.

By

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With 34 Text-figures.

Contents.

I. Petromyzon.

Introduction.

The hypophysis of Petromyzon has been the object of
research of many observers, more indeed than will be referred
to in this paper since complete bibliographies are to be found
elsewhere, and it might almost seem as though any further
work on the same subject could not but be repetition. It
seemed to me, however, when considering the problems
presented by the hypophysis in the light of more recent

research that there are a few points which deserve further attention.

The main outlines of the structure and development of the hypophysis of Petromyzon have been known since the work of Dohrn, Götte, and Scott, and the problems of the hypophysis then presented themselves, but they have been answered in many contradictory ways by them and the many other observers who have devoted their attention to them. Shortly, the main problems are the following:

(1) What is the primitive position of the hypophysis, and has it any primitive relations with the mouth or the nose or any other organs?

(2) What is the primitive method of its development given the great diversity which exists in the vertebrates, and especially the great difference presented by Cyclostomes as compared with almost all other vertebrates?

In this paper I am concerned with these two questions and am led to discuss a few more, such as the relations of the hypophysial cavity to the glandular portions of the pituitary body and the possible presence of one of these portions in Petromyzon corresponding to the pars tuberalis of higher vertebrates.

I wish to express my thanks to Mr. Huxley and Dr. Hogben, not only for stimulating my curiosity in some of these questions but also for useful criticism. To Professor Goodrich also my gratitude is due for helpful advice.

Methods call for no special comment; as complete a series of embryos as possible was studied, cut into serial sections in the transverse, sagittal, and horizontal planes. Stains such as picronigrosin and Lichtgrün were useful in detecting boundaries and limiting membranes where such were obscure. The material of Petromyzon planeri was collected during a stay at Naples, and some stages were supplemented by the kindness of Professor Goodrich. The work was done in the Department of Zoology and Comparative Anatomy at Oxford.

The origin of the hypophysis in Petromyzon from the anterior surface of the head and close to the rudiment of the olfactory organ is familiar in every text-book, after the researches of

Dohrn (1883), Götte (1883), Haller (1896), von Kupffer (1893), Scott (1888), Stendell (1914), Sterzi (1904), and Woerdemann (1914). (To Sterzi's work I have unfortunately been unable to gain access.) It is described as an invagination giving rise to a cavity into which in the adult the olfactory organs open and which extends posteriorly for a considerable distance between the brain and the gut.

In those cases where the hypophysis arises within the stomo-daeum (Selachians and Amniotes) it may develop either as a hollow invagination (Rathke's pocket) or as a solid ingrowth of a mass of cells within which the hypophysial cavity may make its appearance later. Where it arises outside the stomodaeum as in Amia (Reighard and Mast 1908; the writer, see part ii of this paper) or in Amphibia (Götte 1875, Atwell 1919) no invagination occurs, but the rudiment is a solid plate pushing in from the ectoderm. Now the hypophysis of Petromyzon certainly arises outside the stomodaeum, but it is situated next to the region which enlarges enormously during develop-ment, viz. the upper lip. It was my first object to decide whether the so-called invagination is due to the growth of the parts composing its walls or to actual invagination, or to both causes. Pending decision on this point I shall call it the hypophysis depression.
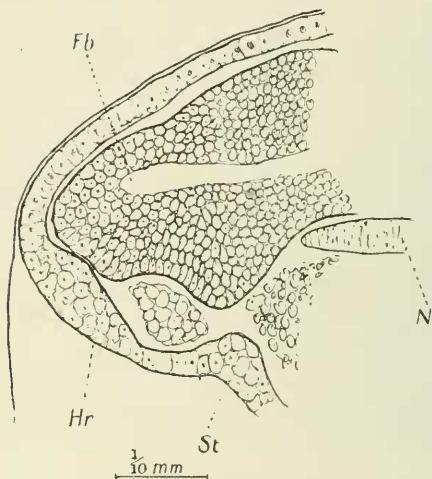
The Hypophysis Depression.

In the earliest stage at which any rudiment of the future organ can be discerned (Text-fig. 1) a thickening of ectoderm on the antero-ventral surface of the head marks the region where the hypophysis and olfactory organs will develop. On the supposed primitive nature of the connexion between these organs I have little to say except that I see no reason for regarding it as anything more than a topographical one, two organs both developing from the ectoderm at the same time and in the same restricted region, viz. the antero-ventral surface of the head of necessity arising together. There is at this stage (just before hatching) no trace of invagination. The stomodaeum is indicated and is separated from the hypophysis

rudiment by a certain distance, occupied by flat ectoderm; there is as yet no upper lip.

In an embryo twelve days old from the time of fertilization (Text-fig. 2), which has consequently hatched, the anterior region of the brain has extended slightly and the antero-ventral surface of the head lies practically horizontal. A depression U-shaped in section near the anterior extremity is the invagina-
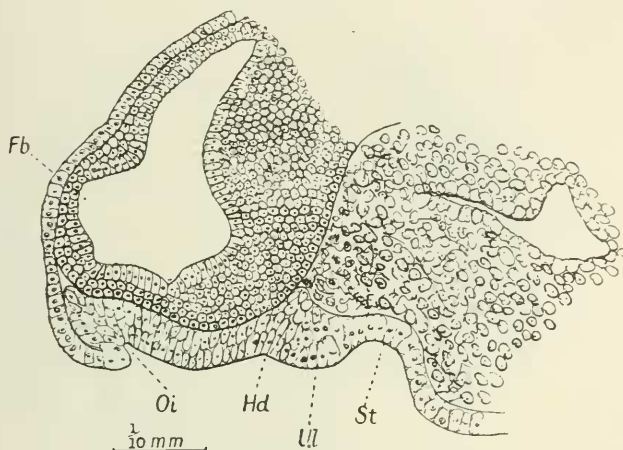
TEXT-FIG. 1.

Petromyzon planeri. Embryo just prior to hatching, rudiment of hypophysis and stomodaeum.

AdO, adhesive organ. A.O., accessory organ. D.W., dorsal wall of fore-gut. F.b., fore-brain. H.c., hypophysial cavity. H.d., hypophysial depression. H.r., hypophysial rudiment. H.s., hypophysial strand. I., infundibulum. L.l., lateral lobes of ' Uebergangsteil '. N., notochord. N.c., cartilage of nasal capsule. O.ch., optic chiasma. O.i., olfactory invagination. O.n., olfactory nerve. P.A., pars anterior. P.E., pineal eye. P.I., pars intermedia. P.N., pars nervosa. S.i.h., solid ingrowth of the hypophysis. St., stomodaeum. T.c., trabecula cranii. U., ' Uebergangsteil '. U.l., upper lip.

tion of the olfactory organ. Farther back is the larger similarly U-shaped invagination of the stomodaeum; but between them is a slight dent on the surface corresponding to a region where ectoderm cells are pushing in beneath the brain. This is the

rudiment of the hypophysis. The region of ectoderm between it and the stomodaeum is no longer flat but convex, being the beginning of the expansion of the upper lip. Is the dent the beginning of a true invagination or is it due to the expansion of the upper lip ? The latter I believe to be the true interpretation. It bears no resemblance to the normal appearance of Rathke's pocket or any invagination, as may be seen by com-

TEXT-FIG. 2.

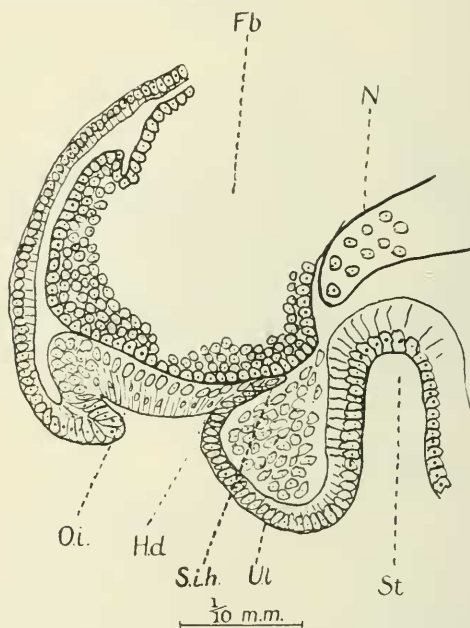Petromyzon planeri. Embryo just hatched, beginning of hypophysis depression.

paring it with the stomodaeum or the olfactory organ. An invagination presents one concave curve ; the hypophysis depression is made up of two convex curves meeting at an apex. There is a solid inpushing of cells at this stage although the depression is a mere dimple, whereas in those cases where the hypophysis arises by invagination it is sunk beneath the surface by means of that invagination which must be almost as deep (see Text-fig. 23 a).

The upper lip continues to increase in size, and the hypophysis depression comes to assume the form of a cleft which deepens and the upper and lower sides of which become more and more parallel as the upper lip enlarges. At the same time the sides of the upper lip grow up with the sides of the anterior

surface of the head so as to leave the hypophysis depression
as a tube which becomes deeper by the lengthening of its walls.
The beginning of this process is shown in Text-fig. 3, and it
is more accentuated in Text-figs. 4 and 5.

The apex of the V, i.e. the limit of the depression, does not
move farther back relatively to the rest of the head.   It never

TEXT-FIG. 3.

Petromyzon planeri.   Embryo fourteen days old,
beginning of expansion of the upper lip.

quite reaches the optic chiasma.   Meanwhile the solid ingrowth
has extended until it almost reaches the tip of the notochord.
To verify this I have resorted to measurements, though I do not
set much store by them owing to the difficulty of measuring
with accuracy and of selecting standard measuring lines since
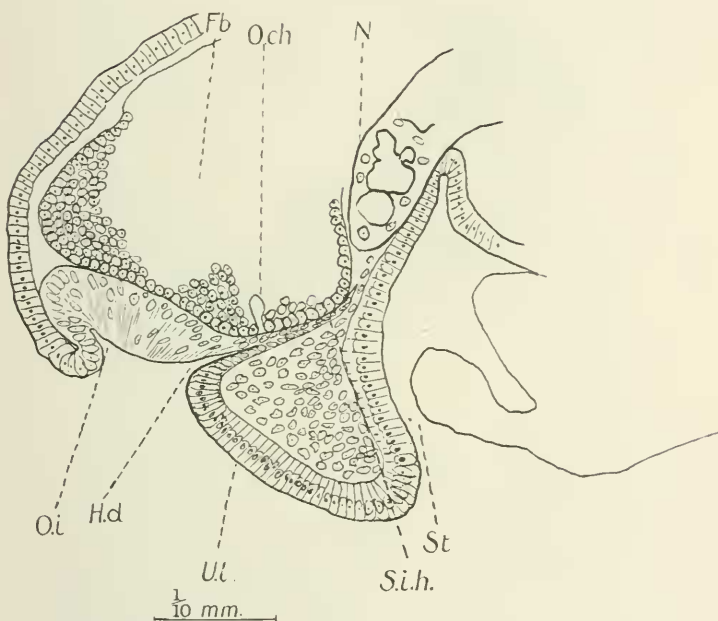no points can be assumed to be fixed.

A. Distance from apex of depression to notochord.

B. Distance from apex of depression to extremity of upper lip.

Embryo represented

In Figures :					A.	B.
3	.	.	.	.	30	15
4	.	.	.	.	30	25
5	.	.	.	.	30	60
6	.	.	.	.	50	120
7	.	.	.	.	80	140
8	.	.	.	.	280	440

TEXT-FIG. 4.

Petromyzon planeri.   Embryo twenty-two days old.

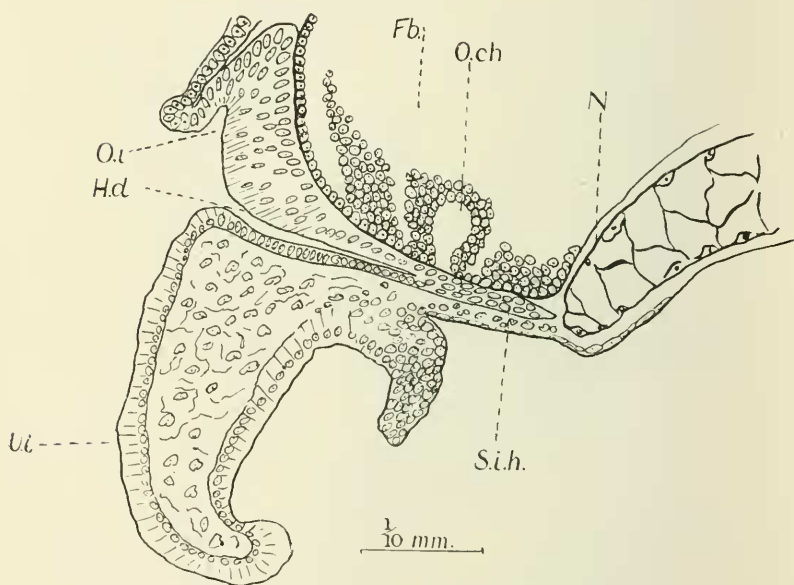Since the measurements are all to the same scale the units are unimportant.

The fact that the distance between the apex of the depression and the notochord does not decrease, while that between the apex and the extremity of the upper lip increases rapidly, supports my contention that the hypophysis depression is not an invagination but is brought about by the relative growth

of the upper lip. The relations of the apex to the optic chiasma confirm this.

The solid ingrowth of the hypophysis extending by itself from the region of the optic chiasma to the notochord does so not by the deepening of the hypophysis depression but by its own lengthening.

It is usually stated that the monorhinal condition of the

TEXT-FIG. 5.

Petromyzon planeri.   Embryo thirty-two days old.

lamprey is due to the connexion of the hypophysis with the olfactory organs which thus communicate with the exterior by means of a single (hypophysial) aperture.   It appears to me to be easier to regard the agent as the upper lip in conjunction with the sides of the anterior surface of the head, which by their expansion cause both organs to be situated in the same secondary depression.
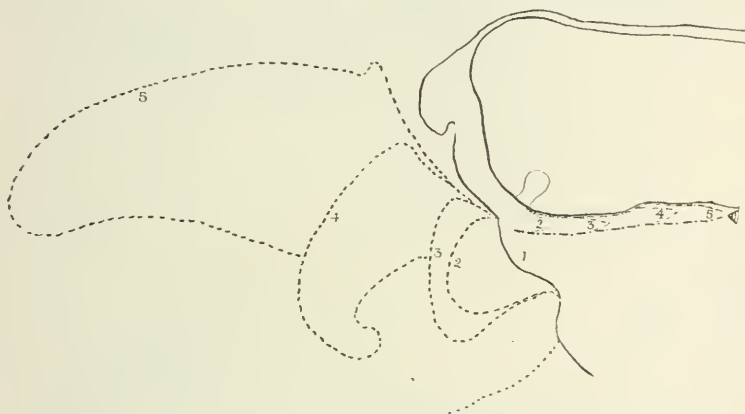
The hypophysis of Petromyzon then belongs to the class of

those which develop by a solid inpushing. A diagrammatic
representation of the growth of the upper lip and formation
of the hypophysis depression is given in Text-fig. 6.

The Formation of the Hypophysial Cavity.

The solid ingrowth lies between the dorsal wall of the gut
and the floor of the brain, separated from them by well-marked
membranes. In the stage represented in Text-fig. 7 no glandular
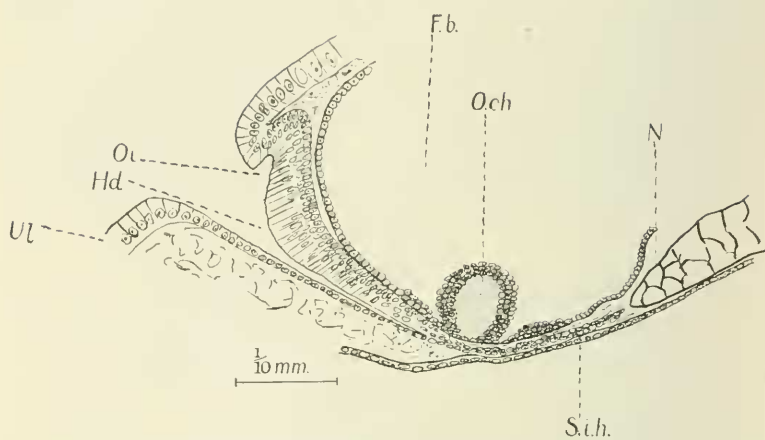
TEXT-FIG. 6.

Petromyzon planeri. Diagram showing the expansion of
the upper lip and formation of the hypophysis depression.

differentiation has as yet occurred. The first indication of the
histological differentiation which will produce the future
pituitary body is to be found in the floor of the brain. Just
dorsal to the posterior portion of the hypophysis a thickening
of the brain-floor occurs composed of neuroglia (Text-fig. 8),
thus foreshadowing the pars nervosa. There is no trace of
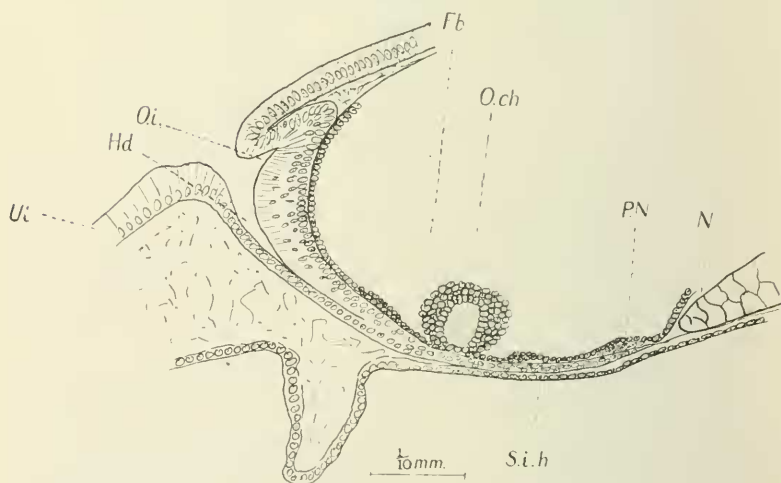hypophysial cavity.

In a later stage (35 mm., Text-fig. 9, and under higher magni-
fication in Text-fig. 10) the hypophysis is beginning to undergo
its histological differentiation (changes which will result in the
formation of the glandular elements which it contributes to the
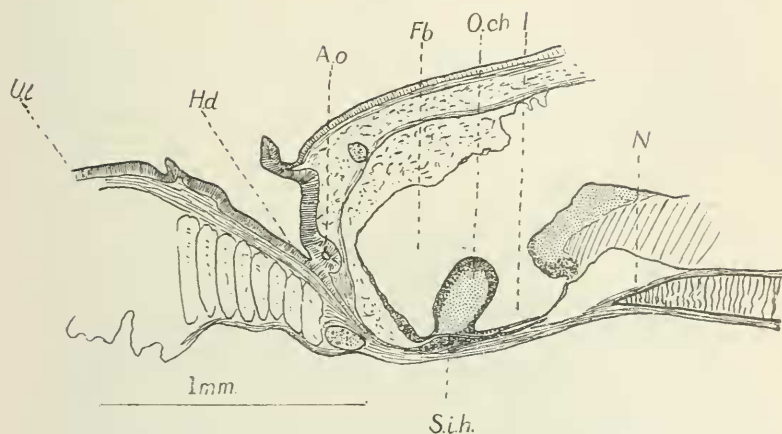pituitary body). Beneath the optic chiasma the strand of tissue

TEXT-FIG 7.

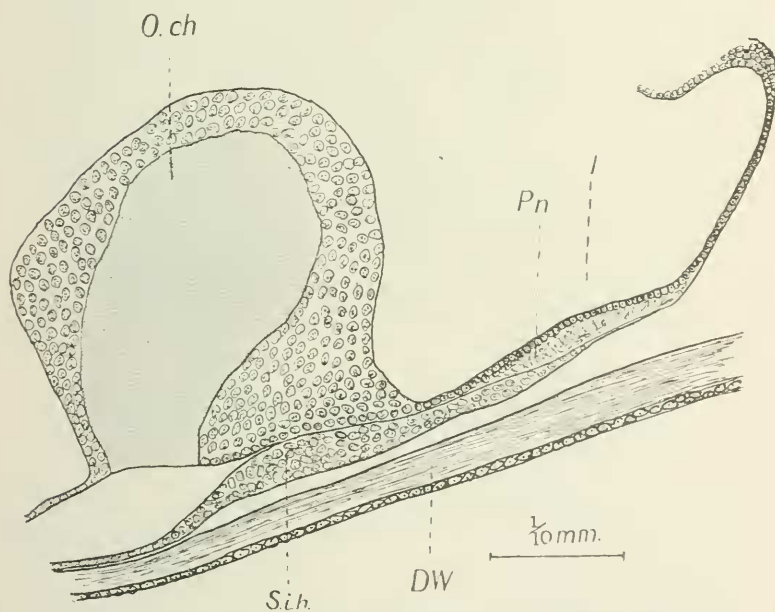Petromyzon planeri. Embryo 10 mm. long.

TEXT-FIG. 8.

Petromyzon planeri. Embryo 15 mm. long. Appearance of
neuroglia thickening in the wall of the infundibulum.

TEXT-FIG. 9.

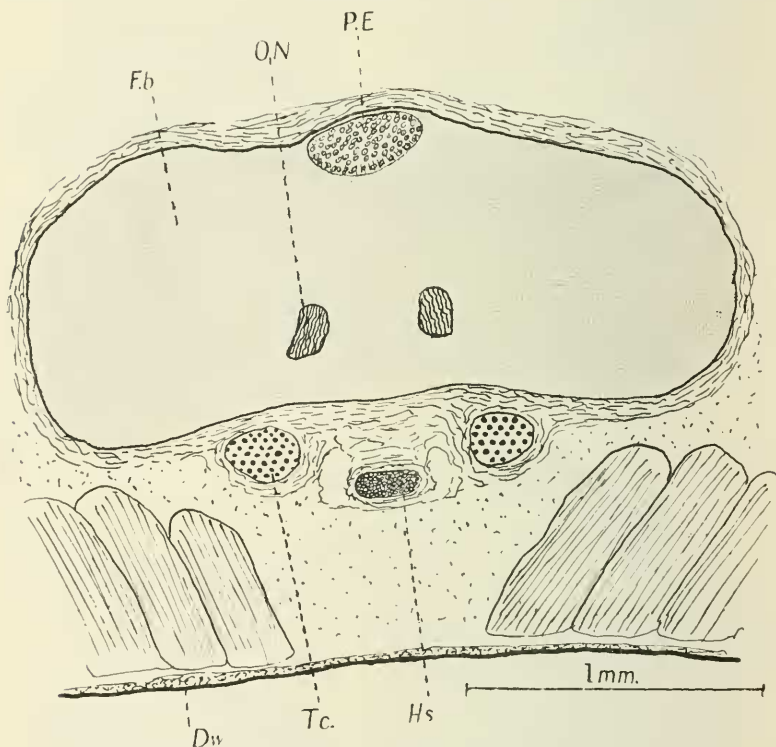Petromyzon planeri.   Embryo 35 mm. long.

TEXT-FIG. 10.

Petromyzon planeri.   The same embryo highly magnified.
Differentiation of the glandular elements.   No trace of a hypo-
physial cavity.

thickens and its cells become ovoid and glandular and less closely packed. Dorsally this thickening is for the greater part of its length closely adpressed to the floor of the infundibulum. The layer of neuroglia which separates the cells lining the infundibular cavity from the outer membrane of the brain-
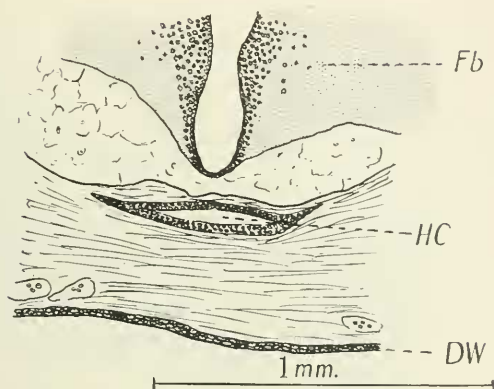
TEXT-FIG. 11.

Petromyzon fluviatilis. Ammocoete. Transverse section just posterior to the apex of the external depression showing absence of hypophysial cavity.

wall has also thickened. All this time the apex of the hypophysis depression has not moved, and the differentiation of the glandular hypophysis takes place from a solid strand of cells, there being still no true hypophysial cavity.
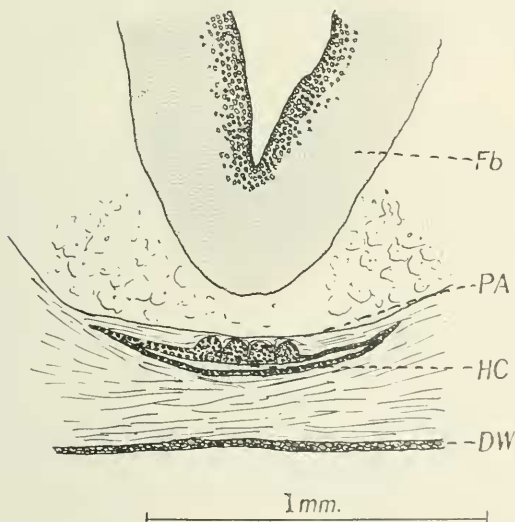
In the Ammocoete a cavity appears in the region just anterior to the gland. It has no connexion with the external depression

TEXT-FIG. 12.

Petromyzon fluviatilis. Ammocoete. Transverse
section slightly farther back and anterior to the gland showing
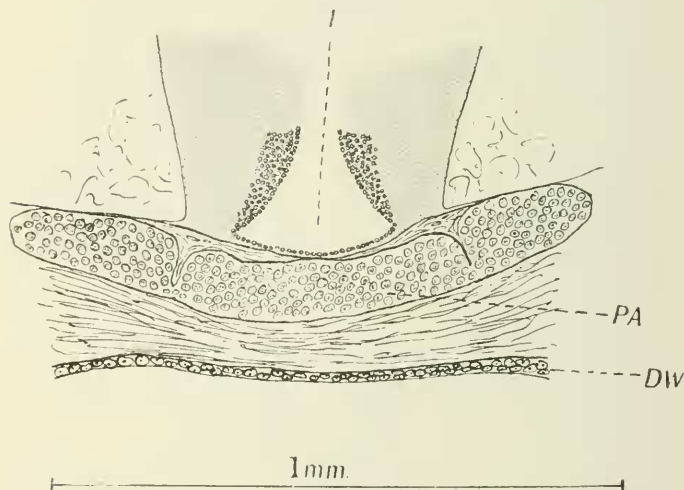the hypophysial cavity in the middle of the hypophysis.

TEXT-FIG. 13.

Petromyzon fluviatilis. Ammocoete. Transverse
section still farther back showing the relation of the gland
to the hypophysial cavity.

(Text-fig. 11) and is hollowed out in the middle of the strand (Text-fig. 12), its walls being two or more cells thick. More posteriorly the cavity extends for some distance ventrally to the glandular body, the latter forming its dorsal wall (Text-fig. 13). It extends farther back laterally than it does in the median plane. Transverse sections posterior to this region show no cavity at all (Text-figs. 14 and 15). The relations of the
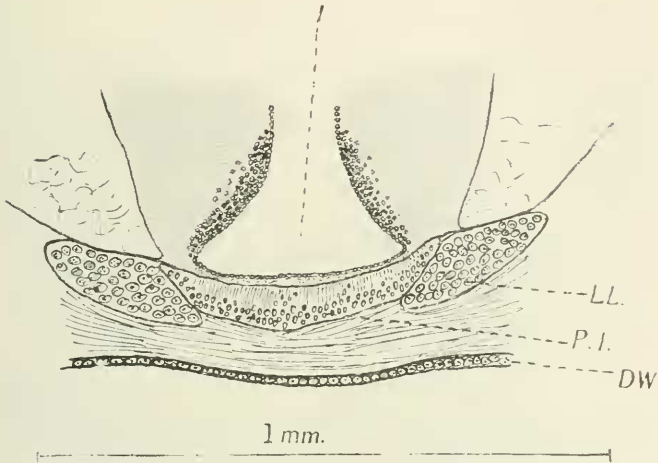
TEXT-FIG. 14.

Petromyzon fluviatilis. Ammocoete. Transverse section behind the limit of extension of the hypophysial cavity showing the lateral lobes of the ' Uebergangsteil '.

hypophysial cavity are shown in Text-fig. 16, which is a sagittal section of an Ammocoete. It arises in the middle of the hypophysis tissue without communication with the hypophysis depression. The glandular tissue forms its dorsal wall, and at this time the pars anterior and pars intermedia, though distinguishable, are in contact, being continuations the one of the other in a straight line. The hypophysial cavity does not separate them. Text-fig. 17 is a high-power view of this stage. The distinction between the parts of the pituitary body

TEXT-FIG. 15.

Petromyzon fluviatilis. Ammocoete. Transverse
section showing the lapping of the lateral lobes back round
the pars intermedia.

TEXT-FIG. 16.

Petromyzon fluviatilis. Ammocoete. Longitudinal section.
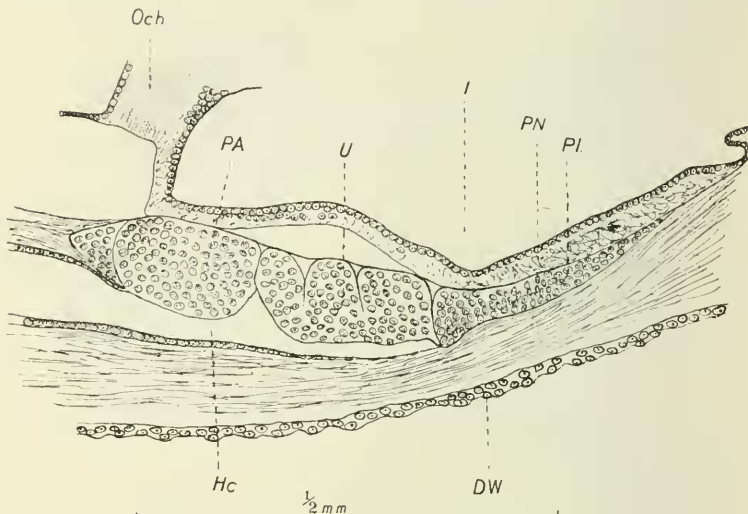
is plain.   Text-figs. 11 to 18 are of P e t r o m y z o n   f l u v i a -
t i l i s , the conditions in p l a n e r i are similar.

At a later stage the hypophysial cavity acquires more definite
walls, and dorsally the wall separates itself from the glands
(Text-fig. 18).   The pars intermedia is the first to lose connexion,
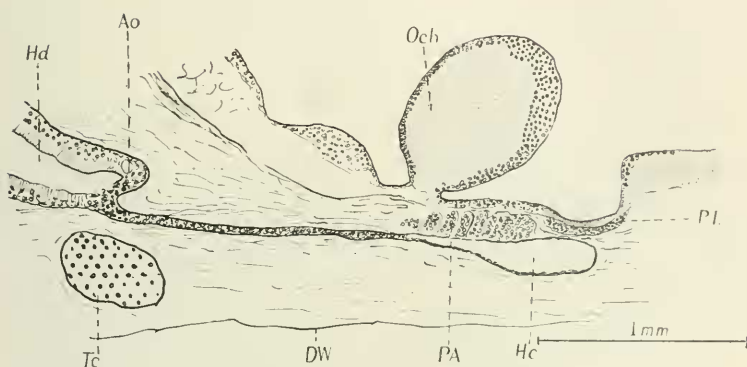a band of connective tissue passing between it and the cavity

TEXT-FIG. 17.

P e t r o m y z o n   f l u v i a t i l i s .   Ammocoete larva more highly
magnified, showing the relations of the hypophysial cavity, the
pars anterior, pars intermedia, pars nervosa, and ' Uebergangsteil'.

and also between it and the pars anterior separating it from
that also.   The pars intermedia, practically devoid of blood-
vessels, is now in intimate connexion with the pars nervosa of
the infundibulum, and its condition is now similar to that
which it presents in the adult.   The pars anterior is highly
vascular.   The cavity becomes more spacious and extends
ventrally and posteriorly.   It acquires a connexion with the
exterior through the hypophysis depression by a split which
occurs along the hypophysis strand.   In the adult (Text-figs. 19,
20, and 21) the separation of the glands from the hypophysial
cavity has gone further and they are now firmly encapsuled

TEXT-FIG. 18.

Petromyzon fluviatilis. Ammocoete. Further extension of the hypophysial cavity and separation from the glands.

TEXT-FIG. 19.

Petromyzon planeri. Adult. Longitudinal section showing the separation of the glands from the hypophysial cavity and the great extension of the latter.

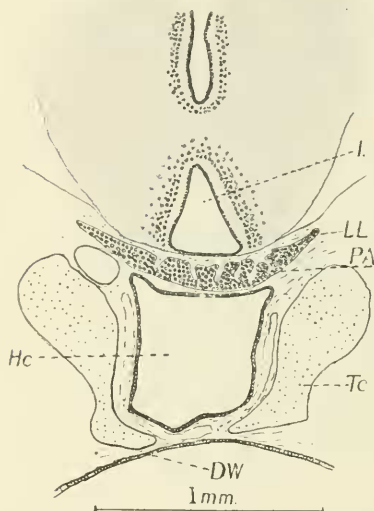in connective tissue. The hypophysial cavity has reached huge dimensions, and is now the well-known sac extending back between brain and gut and communicating with the exterior by the single ' nasal ' aperture.

TEXT-FIG. 20.

TEXT FIG. 21.

Petromyzon planeri. Adult. Transverse section through the pars anterior.

Petromyzon planeri. Adult. Transverse section through the pars intermedia.

Discussion.

The hypophysial cavity of Petromyzon is remarkable for several reasons. Briefly its characteristics may be considered. It develops in the middle of the hypophysis tissue which was a solid inpushing. This is paralleled by many other vertebrates. It remains in connexion with the exterior throughout adult life. This condition is only found elsewhere in Polypterus and Calamoichthys. In these a persisting connexion between the hypophysial cavity and the stomodaeum is referred to by Sedgwick and Wiedersheim, and it would be of great interest to know its development.

The connexion with the exterior may be regarded as a delayed appearance of Rathke's pocket. The adaptive nature of this connexion in Myxine where the hypophysial cavity also communicates with the gut suggests that the hypophysial cavity is secondarily modified, as does also the size of the hypophysial cavity in these forms. The fact that it has lost all connexions with the glandular portions also lends support to this view. For whatever the primitive function of the hypophysis may have been, it was an ectodermal organ sunk beneath the skin and the hypophysial cavity must be supposed to have served to keep the organ in communication with the exterior. In vertebrates above Cyclostomes where a hypophysial cavity exists it is in association with the glandular portions of the organ, though functionless since the latter have adopted the method of internal secretion. In Cyclostomes the cavity is separated from the glands in the adult by a good thickness of connective tissue, although in earlier stages it was in contact with them and they even formed its dorsal wall. It is this fact which enables one to believe that the hypophysial cavity of Petromyzon is homologous with that of other forms, a homology which would be difficult to establish from the adult. But even here Petromyzon is peculiar. In vertebrates typically the hypophysial cavity separates the pars anterior from the pars intermedia. In Petromyzon, as we have seen, the glands differentiate before the appearance of a cavity and the pars anterior and pars intermedia lie in a straight line with the cavity (when it does form) beneath them. Starting from this condition, i.e. the hypophysis arising from the front and growing backwards, and the hypophysial cavity horizontal with the glands on the brain side (dorsal), the pars nervosa of the pituitary very slightly developed and not projecting ventrally; the conditions obtaining in higher vertebrates can be derived when the following changes are taken into account.

(i) The hypophysis grows up from beneath and meets the brain at right angles. The consequence of this is that that portion of the roof of the primitive hypophysial cavity in connexion with the pars anterior which was dorsal and

horizontal in Petromyzon is rotated through 90° and lies anterior and vertical.

(ii) The down-growth of the infundibulum in connexion with the specialization of the pars nervosa forces the pars intermedia down also so that it lies posterior to the hypophysial cavity. In this manner the hypophysial cavity comes to lie between

TEXT-FIG. 22.

Diagram illustrating the difference in relations between the glands and the hypophysial cavity in (*a*) Petromyzon and (*b*) higher vertebrates. Pars anterior dotted, pars intermedia lined, pars nervosa black.

the pars anterior and the pars intermedia. This is shown diagrammatically in Text-fig. 22 ; and it is on such lines that I would explain the difference between the relations of these organs in Cyclostomes and higher forms.

Swale Vincent (1922) gives a figure of the pars intermedia on both sides of the cleft, i. e. his pars anterior is separated from the cleft by a strip of tissue labelled pars intermedia. If the cleft should represent the true hypophysial cavity, this

is incompatible with the theory which I am putting forward here. The strip of tissue in question is probably a portion of the pars anterior the cells of which are slightly modified since

TEXT-FIG. 23.

Diagrammatic comparison between (a) Squalus. (b) Amia. and (c) Petromyzon showing the position of the hypophysis and infundibulum.

here they act as an epithelium and line a cavity. Swale Vincent does not describe this structure in the text, so that not much importance must be placed upon his figure. The

evidence is in favour of the cleft representing the true hypophysial cavity, and to quote Biedl (1913) ' the anterior and posterior lobes are separated by a cleft more or less broad. This represents the vestige of the embryonic hypophysial cavity. The posterior wall of this cavity is directly opposed to the posterior lobe and forms its anterior limit in the shape of a strip . . . known as the pars intermedia.'

The identification of the hypophysis with Kölliker's pit (and therefore the neuropore) of Amphioxus (Willey 1894) is open to the objection that in higher forms hypophysis and neuropore are found in one and the same animal without any connexion.

With regard to the Tunicates the researches of Julin and van Beneden led to these observers believing that the hypophysis is represented by the subneural gland. But the later observations of Willey, Seeliger, and others show that the neural gland is derived not from external ectoderm but from the nervous system. The gland may have some connexion with the neuropore, but later it is in communication with the buccal cavity and a shallow ectodermal invagination (or several) meets the tube growing out of the gland. It is possible that the shallow ectodermal invaginations alone may represent the hypophysis (Stendell 1914*b*). Dr. Hogben kindly permits me to make use of the fact that he found that extracts from the subneural gland of ascidians had no properties such as are present in extracts of the posterior lobe of the pituitary of all classes of Gnathostomes.

Dohrn's (1883) view that the hypophysial cavity of Petromyzon represents a pair of gill clefts is open to the objection that whereas gill clefts are formed by outgrowth of endoderm, the hypophysis is ectodermal.

Haller (1896) believes that the hypophysis of Cyclostomes is secondarily modified, but he describes a lumen in the pars intermedia the existence of which has never been confirmed.

Woerdeman (1914) agrees that the glandular elements are differentiated from a solid strand of tissue in the absence of any cavity, and also that the greatest part (' Grösstenteils ') of the hypophysial depression is due to the overgrowth of the

upper lip. In the hypophysis of Gnathostomes he divides the
hypophysial cavity into three parts ; the most posterior he
terms Rathke's pocket and separated from it by a constriction
he distinguishes the remainder of the cavity as ' Mittelraum '
and ' Vorraum '. Applying these homologies to Petromyzon
he gets the external hypophysis depression to correspond with
the ' Vorraum ', the glandular portion of the hypophysis with
Rathke's pocket, and the upper lip with that region situated
just behind Rathke's pocket in Gnathostomes. The consequence
of this is that the olfactory organs and mouths of Cyclostomes
and Gnathostomes are not homologous. Such conclusions are
unacceptable. The recognition of the secondary nature of
monorhiny, the relations of the olfactory organs to the olfactory
nerves and brain and those of the trigeminal and facial nerves
to the mouth are against his view. Besides, it does not appear
that the acceptance of his divisions of the hypophysial cavity
facilitates their interpretation.

We are left then with the view that the hypophysial cavity
of Petromyzon is homologous with that of other forms but
differs from them by secondary modifications.

The Primitive Position of the Hypophysis.

The most striking feature about the hypophysis of Petro-
myzon at first sight is the fact that it has nothing to do with
the mouth, but communicates with the exterior on the dorsal
side of the head. The latter feature is, as previously stated,
due to the great expansion of the upper lip with the front of
the head, so that when a stage before the upper lip has developed
(Text-fig. 2) is considered, the hypophysis faces ventrally.
But even then it has no connexion with the stomodaeum. The
limits of the stomodaeum are not easy to define since they are
not marked by any structural peculiarity ; but they may be
taken as being the points where the concave curve of the
invagination changes and becomes convex. The fact that in
the majority of vertebrates, viz. Selachians and Amniotes,
the hypophysis develops from within the stomodaeum has

led to the view that this is its primitive position (Stendell 1914 a).

Recently, however, attention has been drawn to those cases where the hypophysis arises outside the stomodaeum and just anterior to it. In this connexion the works of Götte (1915) and Atwell (1919) for Amphibia, of Reighard and Mast (1908) and the writer for Amia, of Wells (unpublished) for Clupeus may be mentioned. In these cases the hypophysis has no connexion with either mouth or nose, and this position Scott (1883) believes to be primitive. Where the hypophysis arises within the stomodaeum, i.e. in Selachians and Amniotes, there is a great development of the fore-brain and cranial flexure ; this rotation of the anterior part of the head causes the ventral elements of the head to lie relatively farther back and accentuates the stomodaeal invagination. This I believe to be the cause of the hypophysis being situated in the stomodaeum in these forms, but the difference between the two types is more apparent than real. In addition there is the fact that the hypophysis is ectodermal tissue which must get into contact with the infundibulum. Where the fore-brain is large and the cranial flexure pronounced this can most conveniently be done through the stomodaeum. But primitively the fore-brain cannot have been large and there was less cranial flexure. This condition is preserved in the Teleosts and Amphibia, and here the typical position for the hypophysis to arise is outside and dorsal to the stomodaeum. Text-fig. 23 is a diagrammatic comparison between Squalus, Amia, and Petromyzon showing the modifications brought about by the fore-brain and the cranial flexure.

Not only are the ventral elements of the head of Squalus pushed backwards, but the dorsal elements are pulled forward owing to the outer side of the curvature of the cranial flexure being dorsal. So the dorsal nerve-roots lead backwards to their respective gill arches whereas in Amia they incline forwards. The anterior position of the heart in Amia is partly due to the embryo being flattened out on the yolk.

Support is lent to the view that this is the primitive position

of the hypophysis by Goodrich's (1917) suggestion that the hypophysis is represented in Amphioxus by the deep groove and depression known as the pre-oral pit in the larva and wheel organ in the adult. This, as its name implies, is anterior to the mouth.

There remains the question as to whether an invagination (Rathke's pocket) or a solid ingrowth is the more primitive method of formation of the hypophysis. It is dangerous in a point of this kind to attempt to induce phylogeny from ontogeny, for the mode of development obeys embryonic conditions. I should suggest that the hypophysis of the primitive vertebrate was an invagination as is the pre-oral pit of Amphioxus, but that when the combination with the infundibulum forming the pituitary body was evolved, the mode of development became influenced by the distance which the ectodermal tissue has to travel.

So in Petromyzon or Amia or Amphibia the ingrowth is solid, in Selachians and Amniotes it tends to be hollow.
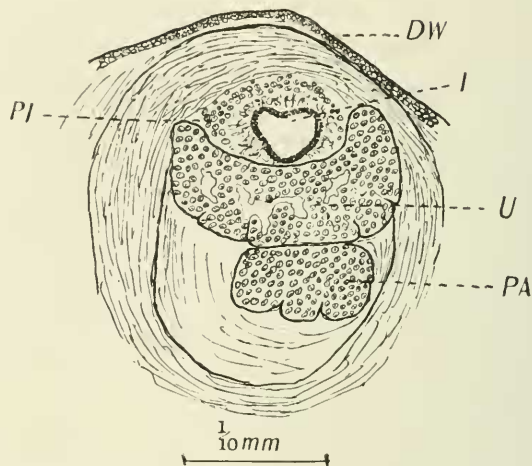
The Pars Tuberalis.

To the description of the main glandular elements of the pituitary body of Petromyzon I have little to add. The pars anterior is made up of two portions, an anterior lobe composed of chromophil cells, and a posterior of chromophobe. This latter portion is termed by Stendell (1914 a) the ' Uebergangs-teil ', by Gentes ' the middle lobe '. Stendell (1913) regards it as morphologically part of the pars anterior (' Hauptlappen ') ; Sterzi as part of the pars intermedia. It is seen in the ammo-coete of Petromyzon fluviatilis in longitudinal section in Text-fig. 17, where it occupies the region between the pars anterior and the pars intermedia. The outer sides of this ' Uebergangsteil ' lap back round the pars intermedia on each side, as seen in transverse section in Text-fig. 15 and in hori-zontal in Text-fig. 24. Text-fig. 25 is a reconstructed view of the whole organ from the ventral surface. This fact was also observed by Woerdeman (1914).

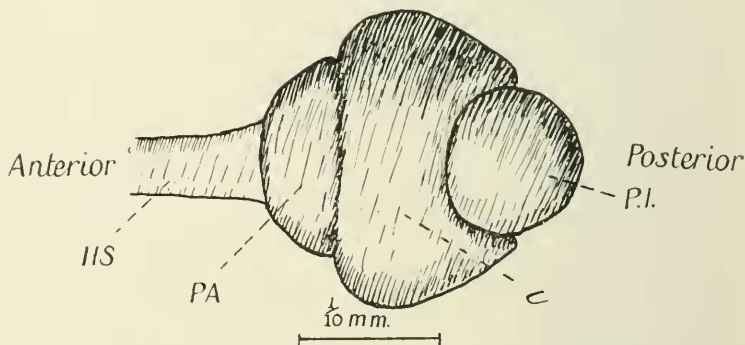Recently attention has been paid to the pars tuberalis as

a distinct element of the pituitary body, notably, by Tilney (1913), Woerdeman (1914), Baumgartner (1916), and Atwell

TEXT-FIG. 24.

Petromyzon fluviatilis. Ammocoete. Horizontal section showing the lapping of the lateral lobes round the pars intermedia.

TEXT-FIG. 25.

Petromyzon fluviatilis. Reconstruction of the pituitary body of an ammocoete seen from the ventral surface after removal of the ventral wall of the hypophysial cavity.

(1919). Woerdeman considers the possibility that its homologue is to be found in the accessory organ (Text-figs. 8 and 9)

situated in the nasal capsule described by Scott (1888). This organ has been studied and is being described by me elsewhere. It develops in close connexion with the olfactory organ and has no histological or topographical similarities with the pars tuberalis of other forms.

In the description of its origin in other forms the pars tuberalis arises as lateral processes (lobuli laterales) which develop acini composed of chromophobe cells, and which are closely adpressed to the brain. According to Tilney it arises in connexion with the pars intermedia (his pars infundibularis). If the pars tuberalis is represented at all in Petromyzon, I suggest that it is the ' Uebergangsteil '. Its cells are chromophobe (Herring, 1910), it has lateral extensions which are closely adpressed to the brain-wall, and is the only part of the organ not otherwise accounted for. From its position between the pars anterior and the pars intermedia it can hardly be said to arise in connexion with the one rather than with the other, though Sterzi considers it to be more closely related to the pars intermdia.

II. Amia calva.

Introduction.

The hypophysis of Amia calva is described by Dean (1896) as developing late. He regarded it as ectodermal, though he admitted that its ventral limit could not be distinguished from the endodermal roof of the fore-gut.

Subsequently Prather (1900) investigated the question and concluded that the hypophysis of Amia was of endodermal origin and derived from the roof of the fore-gut.

Later still, Reighard and Mast (1908), as a result of their researches, believe that Prather was misled in his conclusions by artifacts in his preparations due to shrinking, and they claim that the hypophysis of Amia arises from the ectoderm close to the neuropore, dorsal to and separate from the stomodaeum.

Smith (1914) regards the hypophysis as of ectodermal origin, but thinks that endoderm cells are contributed to it.

Stendell (1914 a) makes no mention of Amia, and remarks that the Ganoids are in need of much further study in this respect. In view of the diversity of opinion on this matter and the fact that the confirmation of either of these two theories must lead to important conclusions with regard to the hypophysis, I determined to examine my preparations of embryonic and larval stages of Amia.

The material consisted of sets of serial sections, sagittal, horizontal, and transverse ; and I may say at once that the remarks made by Reighard and Mast with regard to the care necessary in making the preparations are well founded. By shrinking of the egg-membrane the contained embryo is often compressed and the limits of its organs are sometimes difficult to make out with certainty. Thionin was found to be an efficient stain although it unfortunately fades. For bringing out the basement membranes Lichtgrün or acid fuchsin were found to be useful as counter-stains after safranin and methylene blue.
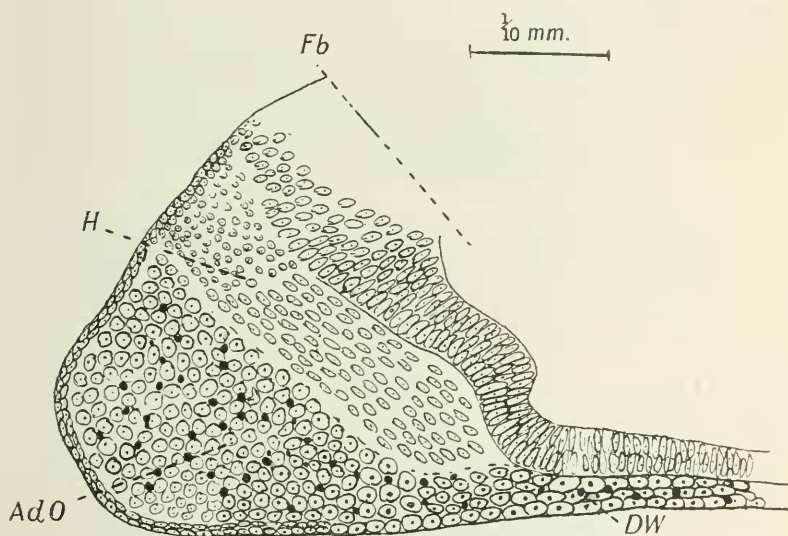
The Origin of the Hypophysis.

The earliest stage in which the hypophysis was visible is shown in sagittal section in Text-fig. 26. The brain is in contact with the antero-dorsal ectoderm in the region where the neuropore has closed. The antero-ventral region of the head is occupied by a mass of large endoderm cells containing abundant yolk and destined to form the adhesive organ. Between the latter and the brain is a tract of smaller cells almost devoid of yolk-granules, in contact with the ectoderm antero-dorsally, and postero-ventrally tapering into a point where the brain comes into contact with the endodermal roof of the fore-gut. There can be no doubt that these cells originate from the ectoderm.

The next stage is shown in small scale in Text-fig. 27 and under higher magnification in Text-fig. 28. The tract of ectodermal cells described in the previous figure is more compressed and denser. Anteriorly it shows traces of previous connexion with the inner layer of superficial ectoderm of the front of the head.

The line of demarcation between it and the underlying endoderm is not easy to see, but with an oil-immersion objective traces of the original basement membrane of the endoderm can be observed. More striking is the difference in yolk content, for whereas the hypophysis (since such I believe these ectoderm cells to be) is practically devoid of it, the endoderm cells both of the roof of the fore-gut and of the adhesive organ contain
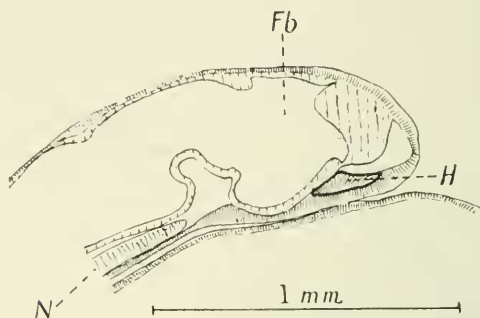
TEXT-FIG. 26.

Amia calva. Young embryo (coiled round the yolk) showing the rudiments of the adhesive organ and of the hypophysis.

numerous large granules. At the same time the brain appears to be pressing down on the hypophysis and squeezing it against the endodermic roof of the fore-gut.

In the next stage (Text-figs. 29 and 30) this pressure has increased, for not only is the hypophysis less thick but it has impressed its convex dorsal and ventral surfaces into the corresponding concavities of the brain and gut-roof. The floor of the brain which in previous stages was bent dorsally in the region of the recessus opticus here continues flat for a further distance forwards. It looks as if the brain and the
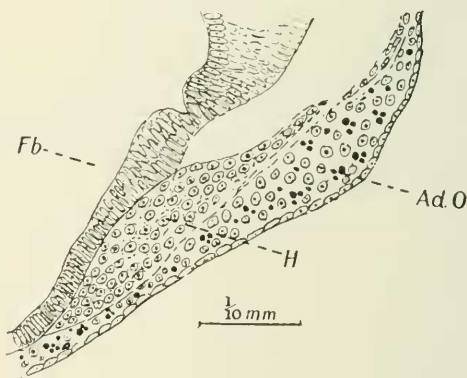
front of the head generally were growing forward and the
hypophysis caught tight between the brain and the gut-roof
were prevented from joining in this forward movement and

TEXT-FIG. 27.

Amia calva. Slightly later stage than the preceding, the hypo-
physis is beginning to lose connexion with its point of origin.
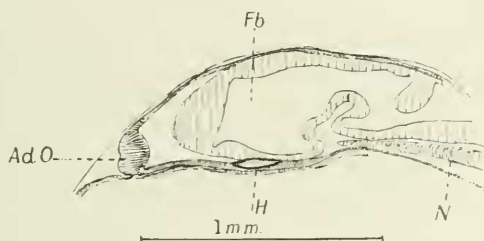

TEXT-FIG. 28.

Amia calva. The same as Text-fig. 27, higher magnification.

so comes to lie relatively farther back. The demarcation
between hypophysis and gut-roof is again hard to pick out,
but the restriction of large yolk-granules to the latter is plain.

As development proceeds the brain and the front of the head
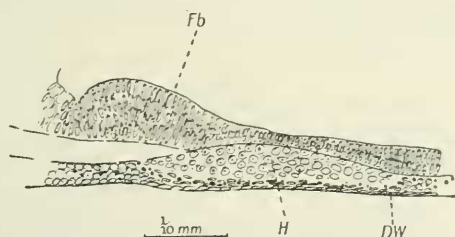generally seems to have grown and extended anteriorly. But

the distance between the hypophysis and the anterior extremity
of the notochord is much reduced.   This may mean that the
tip of the notochord has grown forward, or that the hypophysis
itself has moved back.   The tip of the notochord appears to
be stationary and to bear fairly constant relations to the limits
of the hind-brain, so that the movement must be sought for

TEXT-FIG. 29.

Amia calva, 6 mm. long.   Hypophysis completely separated
from its point of origin and wedged between the brain and
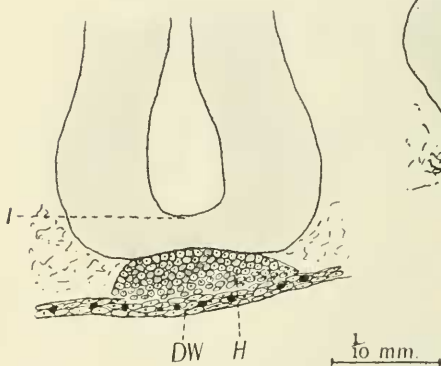the dorsal wall of the gut.

TEXT-FIG. 30.

Amia calva.   The same as Text-fig. 29, higher magnification.

in the hypophysis itself.   Such movement could hardly be due
to active migration since the hypophysis is firmly held between
brain-floor and gut-roof, but is rather to be explained as the
passive result of the movement of the latter.   This movement
may be due to the 'recoil' resulting from the forward growth
of the anterior of the fore-brain as suggested by Reighard and
Mast, or to shrinkage of the gut-roof in the region posterior to
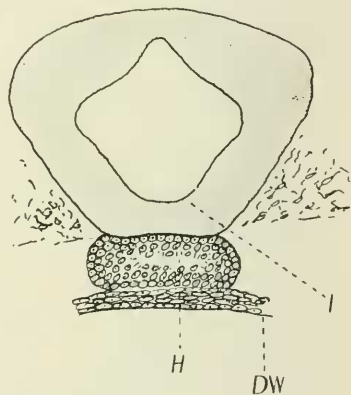the hypophysis, which would have the effect of drawing back

the structures anterior to it. In transverse section the hypophysis about this stage appears as in Text-fig. 31. At first sight it looks as if the hypophysis must have been derived in situ from the underlying endoderm cells. But careful observation with high powers reveals the differences that have been met with before between the cells of the hypophysis and the endoderm cells, viz. absence of yolk and different orientation. In many cases the limiting membrane of the gut-roof

TEXT-FIG. 31.   TEXT-FIG. 32.
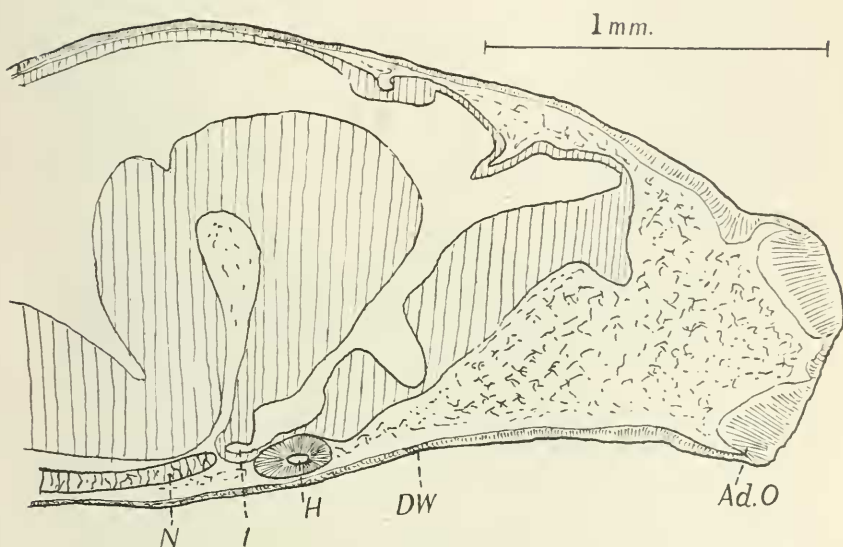

Amia calva. The same as Text-fig. 29. Transverse section.

Amia calva, 8 mm. long. Transverse section. Beginning of the hypophysial cavity.
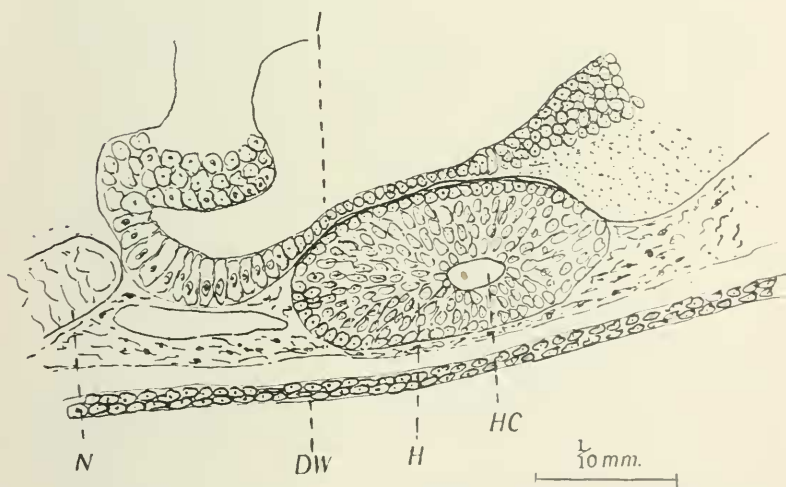
appears to be continuous with that of the hypophysis, and this fact puzzled me for some time, but I believe it to be without significance and due to the close apposition of the hypophysis to the gut-roof. In some sections the real discontinuity of the membrane can be seen. The hypophysis is still in contact with the gut-roof, and at this stage the beginning of the hypophysial cavity can be observed (Text-fig. 32). Mesenchyme begins to make its way between the floor of the brain and the gut-roof, and in the next stage (Text-figs. 33 and 34), where the hypophysis has separated off the endoderm, it is enclosed by a layer of mesenchyme.

TEXT-FIG. 33.

Amia calva. 11 mm. long. The hypophysis with a hypophysial
cavity separated from the dorsal wall of the gut by connective
tissue.

TEXT-FIG. 34.

Amia calva.   The same as Text-fig. 33, higher magnification.

The hypophysial cavity is now distinct with the cells arranged radially around it. There is as yet no distinction between the cells on opposite sides of the cavity, the differentiation into pars anterior and pars intermedia has not yet appeared. On the side of the brain there is no pars nervosa, though the infundibular cavity and the recessus saccularis are already very distinct.

Summary.

1. The hypophysis of Petromyzon arises as a solid ingrowth.

2. The depression in which the hypophysis and olfactory organs come to lie is formed by the great expansion of the upper lip in conjunction with the sides of the anterior surface of the head.

3. The beginning of the histological differentiation of the glandular elements takes place from a solid strand before the appearance of any cavity.

4. The hypophysial cavity arises late as a split in the thickness of the hypophysis, and afterwards extends in both directions communicating forwards with the external depression.

5. The homologue of the pars tuberalis is probably to be found in the 'Uebergangsteil' of Stendell, a chromophobe portion situated between the pars anterior and pars intermedia.

6. The hypophysis of Amia is derived from the ectoderm, thus agreeing with all other known forms.

7. It arises outside the stomodaeum on the anterior surface of the head.

8. It is a solid ingrowth which loses all connexion with its point of origin, and within which the hypophysial cavity makes its appearance at a later stage.

9. Outside and in front of the stomodaeum is probably the primitive position of origin of the hypophysis, without connexion with either mouth or nose.

10. In Selachians and Amniotes where the fore-brain is early very large and the cranial flexure pronounced, the hypophysis arises further posteriorly and so is included in the hollow of the stomodaeum.

11. Although probably primitively hollow, the rudiment of the hypophysis is often solid. Such diversity is brought about by embryonic developmental conditions, perhaps the distance separating the rudiment from the infundibulum.

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